

Use of Shields stress to reconstruct and forecast changes in river metabolism

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SUMMARY

1. Discharge patterns of streams and rivers may be substantially affected by changes in water management, land use, or climate. Such hydrological alterations are likely to influence biotic processes, including overall ecosystem metabolism (photosynthesis and respiration). One regulator of aquatic ecosystem metabolism directly tied to hydrology is movement of bed sediments.

2. We propose that ecosystem metabolism can be reconstructed or predicted for any suite of hydrological conditions through the use of quantitative relationships between discharge, bed movement and metabolism. We tested this concept on a plains reach of the South Platte River in Colorado.

3. Movement of bed sediments was predicted from river discharge and the Shields stress, a ratio of velocity-induced stress to sediment grain size. Quantitative relationships were established empirically between metabolic response to bed movement and recovery from bed movement, thus linking metabolism to hydrology.

4. The linkage of metabolism to hydrology allowed us to reconstruct daily photosynthesis and respiration over the 70-year period for which discharge is known at our study site on the South Platte River. The reconstruction shows major ecological change caused by hydrological manipulation: the river has lost two-thirds of its photosynthetic potential, and the ratio of photosynthesis to respiration is now much lower than it was prior to 1960.

5. The same approach could be used to anticipate ecological responses to proposed hydrological manipulations, to quantify benefits of hydrological restoration, or to illustrate potential effects of change in climate or land use on flowing-water ecosystems.

Keywords: disturbance, photosynthesis, respiration, Shields stress, stream metabolism

Introduction

Water management changes the mean, frequency distribution, and seasonal sequencing of discharge in streams and rivers; changes in land use and climate can

have similar effects (Schindler, 1997; Foley *et al.*, 2005). While even small changes in discharge may affect water velocity and induce measurable ecosystem responses (Horner & Welch, 1981; Poff, Voelz & Ward, 1990), the most notable threshold for ecological response to a change in flow corresponds to movement of the bed (Uehlinger, Buhner & Reichert, 1996; Uehlinger & Naegeli, 1998; Biggs, Smith & Duncan, 1999; Biggs, 2000). Movement of the bed can be expected to cause abrupt changes in metabolism and distribution of the biota in streams and rivers, as bed movement disrupts the stability of metabolically active biofilms and

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displaces organisms (Peterson *et al.*, 1994; Biggs, 1995; Uehlinger *et al.*, 1996; Uehlinger & Naegeli, 1998; Biggs *et al.*, 1999; Biggs, 2000). In a given reach of river or stream, the shear stress (force per unit area applied to the bed) can be estimated from discharge if the geometry, slope, and roughness of the channel are known. When information on shear stress is combined with measurements of particle size, movement of the bed can be predicted for specific points or mapped over the entire bed for any specific volume of flow (discharge).

To the extent that ecological responses are generated by bed disturbance, the relationship between shear stress and discharge for a given reach of river or stream could provide a means for reconstructing or predicting certain ecological responses to changes in water management, land use, or climate. We tested this possibility on a reach of the South Platte River located approximately 50 km below Denver, Colorado, for which a long record of flow is available (Fig. 1). Through mapping of shear stress and development of empirical relationships between bed movement and rates of metabolism, it was possible to link metabolism to hydrology and reconstruct daily photosynthesis and respiration over the 70-year period for which discharge is known for our study site on the

South Platte River. Thus, we were able to evaluate the effects of water management practices on ecosystem metabolism for the South Platte.

Methods

Study area

The South Platte River drains an area of approximately 63 000 km² in Colorado, Wyoming and Nebraska (Fig. 1). The hydrograph for the South Platte is dominated by snowmelt runoff, which typically peaks in early May, but brief spates following thunderstorms (mostly from May to September) are common. The waters of the South Platte are now intensively managed through a network of reservoirs and ditches that in combination provide storage and delivery of water for municipal and agricultural use. In addition, the South Platte below Denver carries transmountain diversion water from the Western Slope of the Colorado Rocky Mountains (Saunders & Lewis, 2003). Wastewater from the city of Denver is a major source of nitrogen and phosphorus to the river but, downstream of Denver, agriculture also is an important source of nutrients.

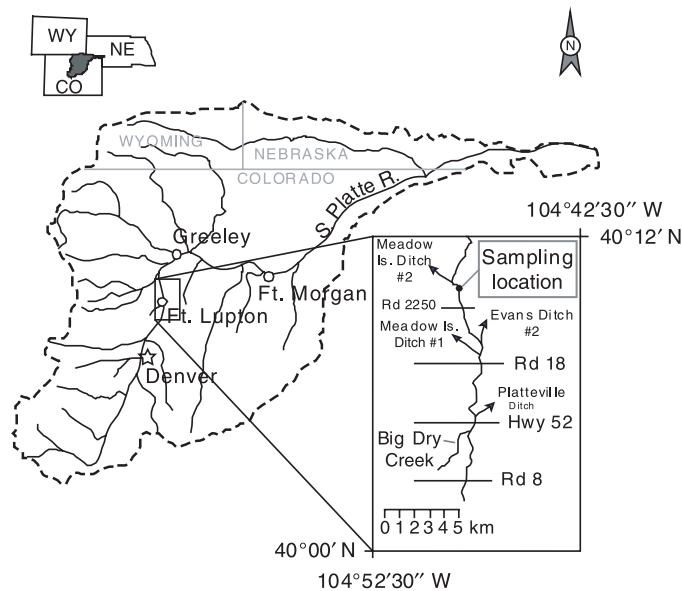


Fig. 1 Map of the South Platte River basin showing the study area (left) and a photograph showing the river channel within the study area (right).

The study site (McCutchan *et al.*, 2003; Pribyl *et al.*, 2005) is located near Ft. Lupton, Colorado, 55 km downstream (north) of Denver (40°9'47"N, 104°48'50"W); the drainage area above the study site is approximately 13 000 km². Flowing at gradient of approximately 0.001 m m⁻¹, the South Platte below Denver forms a mildly sinuous channel that is typically 40–60 m wide; average flow depth ranges from about 20–50 cm and discharge typically is 2–40 m³ s⁻¹. The channel is partially shaded in summer by plains cottonwood (*Populus deltoides*) and willows (*Salix* sp.) and the substrate at the site is composed of sand and fine gravel (Pribyl *et al.*, 2005). Benthic algae colonize the substrate along the margins of the river during periods of low discharge; during extended periods of low flow, filamentous algae and biofilms may cover much of the wetted channel but are easily disturbed when flow rises during snowmelt or following summer thunderstorms.

Nutrient concentrations near the study site are high and show strong seasonal trends. During the study period, the nitrate concentration was higher during the cool months (October–April) than during the warm months (May–September), but nitrate was abundant year-round (Fig. 2). The concentration of ammonia-N generally was high during the cool months, but remained below 0.5 mg L⁻¹ from May through September. The concentration of total dissolved phosphorus typically was higher during the cool months than during the warm months, but the concentration was never low during the study period (Fig. 2).

Shields stress

Within the study reach, information was collected as necessary to map shear stress, τ , and measure the distribution of grain size over the streambed. Bed topography within the 140-m reach was measured with a total station (electronic theodolite; Fig. 3). The bed sediment was sampled at six randomly selected locations to determine the range of grain sizes available for transport as bed load. An additional sediment sample was taken from a nearby borrow pit to determine the grain size of older alluvial deposits, which appear to be similar to the sediment presently forming the channel bed. Stage height was measured with an automated water-level logger (Global Water, Model WL15; <http://www.globalw.com>). Power

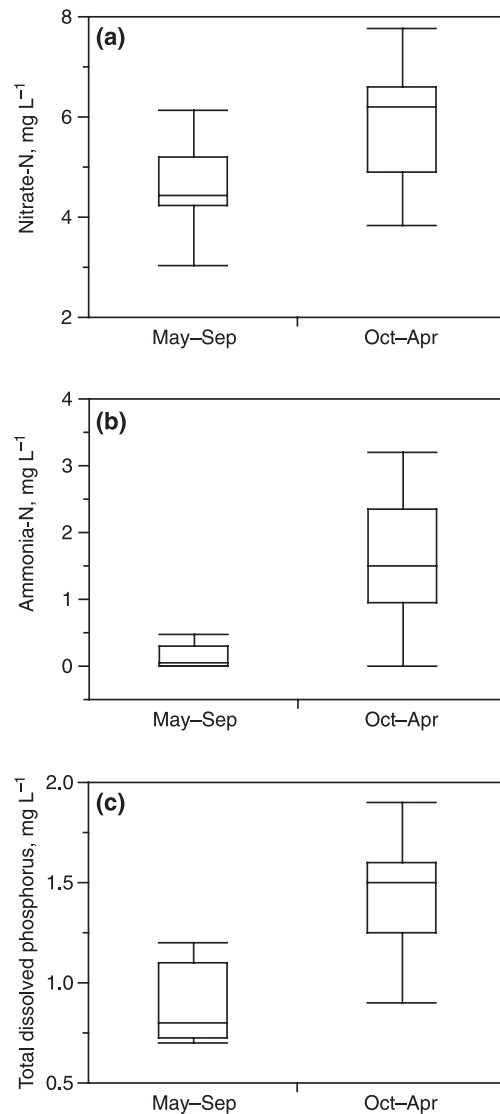


Fig. 2 Concentrations of nitrate-N (a), ammonia-N (b) and total dissolved phosphorus (c) for the South Platte River during the study period. Boxes show medians, 25th percentiles and 75th percentiles; whiskers show ranges of concentrations. Data are from Pribyl (2002) and from the Denver Metro Wastewater Reclamation District.

functions calibrated against depth–velocity profiles were used to estimate discharge, average depth and width of the wetted channel from stage height; the equations were re-calibrated routinely to account for changes in channel geometry. Depth–velocity profiles were made approximately once per month or after periods of high discharge when changes in geomorphology were expected. On each date, measurements were made at one to five cross sections within the

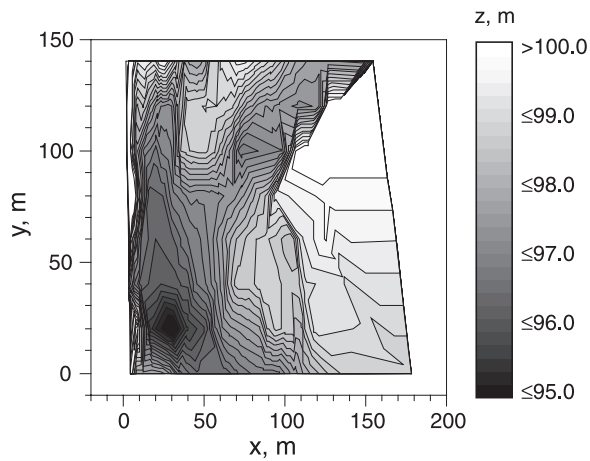


Fig. 3 Map of bed topography within the study area (15 October 1999).

study reach, and measurements of depth and velocity for a given cross section were typically made at 2-m intervals.

Shear stress was estimated as follows:

$$\tau = \rho ghS \quad (1)$$

where ρ is the density of water, g is the gravitational acceleration, h is the flow depth and S is slope. The shear stress varies spatially due to differences in bed topography (Lisle *et al.*, 2000), and it varies temporally due to changes in discharge. Estimates of shear stress for different flows were made here by subdividing the channel into sections of uniform depth, assuming a constant reach-average slope, $S = 0.0010$. Water-surface elevations were measured over a range of flows to verify this assumption. Local depths were determined in the process of cross-sectional surveys and measurements of discharge. The threshold for bed movement can be judged by use of the Shields stress, a dimensionless ratio of bed shear stress to grain size,

$$\tau^* = \tau / [(\rho_s - \rho)gD_{50}]^{-1} \quad (2)$$

where τ is shear stress at the sediment–water interface, ρ_s is the density of sediment and D_{50} is the median grain size of the bed sediment. The bed sediment begins moving when the local Shields stress, τ^* , exceeds what is termed the critical Shields stress, τ^*_c . Results from field and laboratory studies indicate that the critical Shields stress for D_{50} generally lies within the range 0.03–0.06, with the range determined by several factors, including grain Reynolds number,

grain size and sediment sorting (Buffington & Montgomery, 1997). The bed sediment of the South Platte River is moderately well-sorted; thus, a value of $\tau^*_c = 0.045$ is assumed in estimating the threshold for transport. Using the relations between discharge, depth and slope, and assumptions about the channel geometry, it is then possible to calculate the proportion of the bed that is in motion for any given discharge.

Estimation of algal biomass

On a single date in October 2003, algal biomass within the study reach was measured as Chlorophyll *a*. Samples of the upper 2–3 cm of sediment were collected with a small (1.5 cm diameter) coring device at 5-m intervals along three transects across the channel. Concentrations of chlorophyll *a* were measured by sonication and hot-ethanol extraction followed by spectrophotometry (Marker *et al.*, 1980; Nusch, 1980; McCutchan, 1999).

Estimation of stream metabolism

Field studies of ecosystem metabolism were conducted by an open-channel method that provides estimates of photosynthesis and respiration on a reach-wide basis through a mass-balance accounting for oxygen (Odum, 1956; Uehlinger & Naegeli, 1998; McCutchan *et al.*, 2002; Ortiz-Zayas *et al.*, 2005). Estimates of metabolism were calculated from measurements of temperature and dissolved oxygen concentration at a single station on 106 dates between June 2000 and March 2003. On each date, measurements of temperature and dissolved oxygen were made at 10-min intervals with a Hydrolab Datasonde 4 (<http://hachenvironmental.com>); prior to each deployment, the oxygen sensor was calibrated in well-stirred water equilibrated in ambient air. Typically, barometric pressure was measured at 10-min intervals with a high-precision Barometer (Honeywell International, Model HPB 200; <http://ssec.honeywell.com>). On some dates, pressure was interpolated from hourly measurements of pressure at Denver International Airport (DIA; approximately 25 km from the study site) after correction for the difference in elevation between DIA and the study site; pressure data for DIA were obtained from the National Climatic Data Center.

Propane was used as a volatile tracer to estimate the reaeration coefficient for oxygen (Kilpatrick *et al.*, 1989; Pribyl *et al.*, 2005). Reaeration coefficients were adjusted for temperature as follows (Thomann & Mueller, 1987):

$$k = k_{20}1.024^{(T-20)} \quad (3)$$

where k_{20} is the reaeration coefficient for oxygen at standard temperature (20 °C) and T is the temperature at which the reaeration coefficient was measured. After adjustment to a common temperature, the reaeration rate coefficient for oxygen did not vary significantly with discharge among six separate estimates (Pribyl *et al.*, 2005). Reaeration coefficients were also measured on 21 dates for nearby reaches of the South Platte River below Denver (Denver Metro Wastewater Reclamation District, unpublished data); after correction for temperature, slope of the channel explained a substantial fraction of the variation in reaeration coefficients in the vicinity of the study reach ($r^2 = 0.74$, $P < 0.0001$), as follows:

$$k_{20} = 474S^{0.603} \quad (4)$$

Neither discharge nor depth added significantly to the predictive power of the relationship between slope and reaeration coefficient; thus, the median reaeration coefficient for the study reach (12.5 day⁻¹ at 20 °C) was applied to all dates.

Estimation of metabolism can be affected by flux of groundwater to the channel (McCutchan *et al.*, 2002). The rate of groundwater seepage (m³ day⁻¹ m⁻¹ or m² d⁻¹) was estimated with a relationship developed from the record of flow residuals (after correction for withdrawals and tributary inflows) between two upstream gages (USGS 068020500 at Henderson and USGS 06721000 at Ft. Lupton; Pribyl *et al.*, 2005). Rates of seepage for each date were divided by channel width (m) to obtain rates of groundwater flux per unit area (Q_g/A , m day⁻¹). The concentration of oxygen associated with groundwater flux (C_g , mol O₂ m⁻³) was estimated from samples collected from shallow alluvial wells adjacent to the sampling reach. No seasonal trend was observed for the concentration of O₂ in alluvial wells, so the mean concentration for all the alluvial samples (0.148 mol O₂ m⁻³) was used in the calculation of metabolic rates (see below) on all dates.

For each deployment of the recording multiprobe, rates of metabolism were calculated at 10-min inter-

vals according to the following equation (McCutchan *et al.*, 2002; McCutchan & Lewis, 2006):

$$P + R = \frac{1}{e^{kt} - 1} \left[\frac{C_t k \left(\frac{Q_g}{A} t + z_0 \right)}{e^{-kt}} - S \frac{Q_g}{A} (1 - e^{kt} + kte^{kt}) - kz_0 (C_0 + S(e^{kt} - 1)) \right] - C_g \frac{Q_g}{A} \quad (5)$$

where $P + R$ is the rate of net ecosystem metabolism (the sum of photosynthesis and respiration), C_t is the oxygen concentration at time t , t is the measurement interval or the travel time for the implicit reach (10 min), C_0 is the oxygen concentration at time 0, z_0 is depth at time 0 and S is the saturation concentration for oxygen.

Daytime rates of R were estimated from nocturnal rates of net ecosystem metabolism and changes in temperature, based on the assumption that $Q_{10} = 2$. Rates of P were then calculated as the differences between net metabolism during daytime and the estimated daytime rates of R .

When open-channel estimates of stream metabolism are based on measurements at a single station, the implicit reach-length for calculation of metabolism will change if discharge (flow velocity) changes (McCutchan & Lewis, 2006). If reach-length changes and depth varies upstream of the station where measurements of oxygen concentration are made, changes in discharge can result in errors in estimates of metabolism if a constant average depth is assumed for each sampling date; changes in the reaeration coefficient upstream of the sampling location can also affect the estimation of metabolism if reach-length changes. To test the assumption that changes in discharge did not affect estimates of metabolism in this way, bed topography and channel slope were measured within a 13 km reach spanning from Highway 52 (12.5 km upstream of the sampling location) to the Meadow Island no. 2 ditch (just downstream of the sampling location; Fig. 1). Within the 13 km reach, channel cross-sections were measured at intervals of approximately 300 m and slopes between cross sections were calculated from changes in elevation on 7.5-min topographic maps (U.S. Geological Survey).

Reconstruction of metabolism

A 70-year record of daily mean discharge is available for a gage located at Ft. Lupton (USGS 06721000), just

upstream of the study site. This long record of flow makes possible the reconstruction of ecosystem metabolism for the South Platte River from relationships between flow, sediment movement and ecosystem metabolism. The results of field studies of metabolism were used to develop relationships between bed movement and rates of ecosystem metabolism. Thus, the relationship between discharge and bed movement made it possible to relate hydrology to ecosystem metabolism over the 70-year period of the flow record.

Results

Field observations and survey measurements taken during 2000 and 2001 indicate that floods of short duration are capable of reworking the bed surface to depths of up to approximately 30 cm (Fig. 4). Typically, the volume of sediment eroded by floods from one portion of the channel is balanced by deposition elsewhere; thus, the channel appears to be stable in the near-term. If discharge remains stable following a flood, the main body of the flow reverts into a narrower channel that is 1/2 to 1/3 of the bank-full width. However, because of continued shifting of the bed and bars, small fractions of the flow remain distributed over low-lying bar surfaces. A coarse surface layer (armour) generally forms in these areas, which are characterized by relatively shallow flow and low shear stress. Armour layers in the South Platte River are discontinuous and stable only in the short term; under typical summer conditions, however, the sediment forming these surfaces remains stable for a few weeks at a time, allowing the growth of attached algae.

Measurements taken in 2000 and 2001 indicate that the substrate stabilizes to form an armour layer

wherever the water depth is less than approximately 0.20 m. This is approximately the point where we expect the bed sediment to come to rest, based on the Shields criterion for initiation of motion. Knowing D_{50} and given a specific value of τ_c^* , Eqn 2 can be solved to find the threshold shear stress below which the bed is stable; Eqn 1 then can be solved to find the critical flow depth, h_c , below which there should be very little transport of bed load. Using a value of $\tau_c^* = 0.045$ (Buffington & Montgomery, 1997), the measured values of $D_{50} = 0.0027$ m and $S = 0.001$ m m⁻¹, and appropriate values for the constants, we find that $h_c \approx 0.20$ m. If the depth is much greater than 0.2 m, the bed sediment should be in motion and biomass of attached algae cannot develop; if the depth is lower than this value, the substrate should be stable and algal biomass will develop accordingly.

At flows above approximately 11 m³ s⁻¹, the depth of flow exceeds the critical depth for bed movement over most of the wetted channel and the bed will be stable only within a narrow band at the margin of the channel. During any brief surge in discharge (e.g. following a thunderstorm), stable portions of the bed will exist at the margin of the channel; during a spate, however, stable areas of the bed may not have been inundated for a sufficient length of time to support significant growth of algae. Thus, the expected areal rate of photosynthesis is near zero any time the flow exceeds approximately 11 m³ s⁻¹.

Estimation of algal biomass

Periphyton sampling showed that algal biomass was low (<2 mg Chl *a* m⁻²) where the depth was greater than approximately 0.2 m, and about half of the measurements in water deeper than 0.2 m were near

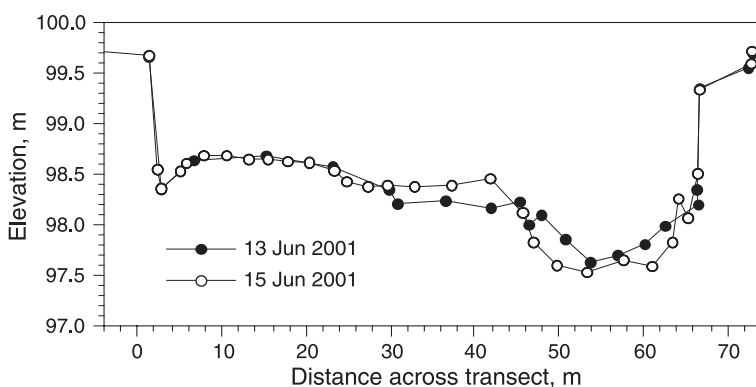


Fig. 4 Cross section of the bed before (13 June 2001) and after (15 June 2001) a flow of >20 m³ s⁻¹.

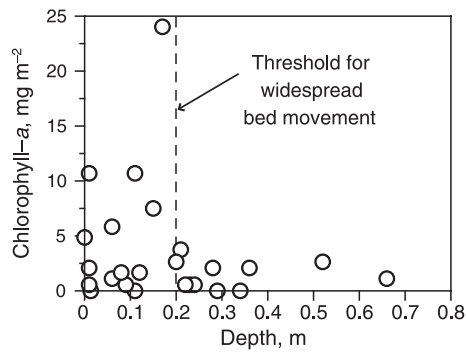


Fig. 5 Concentrations of chlorophyll *a* for attached algae on 12 October 2003.

zero (Fig. 5). Where the depth was <0.2 m, concentrations of chlorophyll *a* spanned a much broader range. Some of the measurements in shallow water were <2 mg Chl *a* m^{-2} , but concentrations in shallow water on this date ranged as high as approximately 25 mg Chl *a* m^{-2} .

Measured rates of metabolism

Relatively few measurements of ecosystem metabolism were made during the cooler months (October–April) and, during winter, the rate of photosynthesis typically was near zero, regardless of the time since disturbance. Although it is clear that rates of photosynthesis during winter were affected by low temperatures and reduced light availability, the limited number of measurements during the cooler months prevented a rigorous analysis of the effect of bed disturbance on rates of metabolism (or the sequence of recovery for metabolism) across the entire year. Even if additional measurements had been made during the cool months, limitation of photosynthetic rates by light and temperature may have obscured effects of bed disturbance on rates of metabolism during the cool months. For these reasons, analyses and reconstructions of metabolic rates are limited to the warm months (May–September).

Field measurements of ecosystem metabolism showed that photosynthesis declined as the flow approached 11 m^3 s^{-1} and was suppressed to negligible rates whenever discharge exceeded 11 m^3 s^{-1} (Fig. 6). Respiration was only weakly affected by change in discharge and did not show such a clear threshold (Fig. 5). The rate of photosynthesis depended on the amount of time elapsed since the most

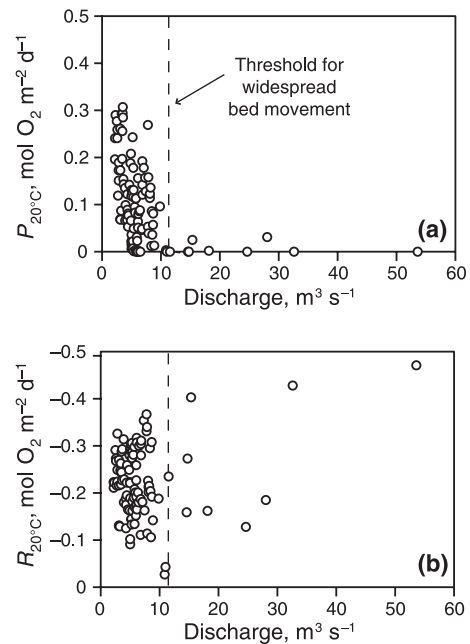


Fig. 6 Relationship between rates of photosynthesis (a) and respiration (b) and discharge in the study reach of the South Platte River, 2000–2003. Rates are corrected to a common temperature of 20 $^{\circ}C$ (Q_{10} for the correction = 2.0).

recent episode of bed movement; respiration showed a similar pattern, but the relationship with time since the last disturbance was weaker than the relationship for photosynthesis (Fig. 7). Also, in the first week after a spate, rates of respiration were much more variable than rates of photosynthesis (Fig. 6).

For this study, the implicit reach length for calculation of metabolic rates was 141 m at a discharge of 1 m^3 s^{-1} and 373 m at a discharge of 11 m^3 s^{-1} . Thus, at the highest discharges measured during this study, the implicit reach-length was somewhat longer than the reach where detailed measurements of bed topography were made (Fig. 3). Upstream of the reach where detailed measurements of bed topography were made, the mean depth of the channel increased slightly (approximately 15%) over the next 900 m; farther upstream within the 13 km reach, the channel is considerably narrower and deeper. For more than 2 km above the sampling location, the slope of the channel varied little and the estimated reaeration coefficient (Eqn 4) within this reach varied by $<2\%$; farther upstream, reaeration coefficients are highly variable because of natural changes in the slope of the river bed and also pools and drops associated with diversion structures.

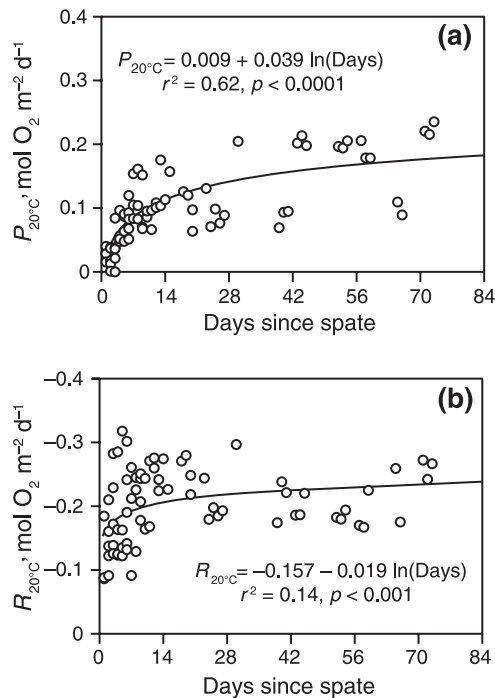


Fig. 7 Relationship between elapsed time since widespread disturbance of the bed (i.e. discharge $>11 \text{ m}^3 \text{ s}^{-1}$) and the rate of photosynthesis (a) and respiration (b). Rates are corrected to a common temperature of $20 \text{ }^{\circ}\text{C}$ (Q_{10} for the correction = 2.0).

Historical reconstruction of metabolism

The effects of bed movement and the time course of change following an episode of bed movement provide a basis for reconstructing potential photosynthesis, respiration and the ratio between the two from the long historical record (70 years) of flow that is available for the South Platte River below Denver. Reconstruction carries the implicit assumption that the geomorphology and sediment grain size of the study area have not changed greatly over the 70 years of record. The presence of very old trees on the river bank (Fig. 1) and the grain size of older alluvium ($D_{50} = 0.0034 \text{ m}$) support these assumptions. Examination of aerial photographs and satellite imagery provides further information on the stability of the channel just upstream of the sampling location, but such information covers only the last few decades.

Changes in concentrations of nutrients and organic matter over time can affect the mean rate of metabolism regardless of flow regime. As the South Platte has very likely been nutrient-saturated for at least 70 years because of its association with agricultural

and municipal nutrient sources since the late 19th century, change in nutrient status probably is not a major factor in the present case. For the South Platte River or for other flowing waters, there are very few records of nutrient concentration pre-dating the 1960s. The Colorado Department of Public Health and Environment (CDPHE) and the Denver Metro Wastewater Reclamation District (MWRD) have monitored the water chemistry of the South Platte since the mid-1960s. At a station approximately 20 km upstream of the sampling reach for this study (i.e. nearer to Denver), ammonia concentrations were higher prior to 1990 (median 8.2 mg N L^{-1}) than in more recent years (median 3.5 mg N L^{-1}), but nitrate concentrations have increased somewhat since 1990 (median 1.0 mg N L^{-1} before 1990; median 4.3 mg N L^{-1} after 1990); the net effect of these changes has been a slight decrease in the concentration of total inorganic nitrogen (TIN), although TIN has remained consistently high over the period of record (CDPHE and MWRD, unpublished data). The concentration of total dissolved phosphorus at this monitoring station also has remained high over the period of record (median 2.4 mg L^{-1} before 1990; median 1.7 mg L^{-1} after 1990). Biological oxygen demand (5 days, $20 \text{ }^{\circ}\text{C}$) was higher before 1990 (median 12 mg L^{-1}) than in more recent years (median 8 mg L^{-1}), but a reduction in the rate of nitrification associated with the observed decline in ammonia concentrations may account for a large part of the decline in biological oxygen demand.

At sites where a change in nutrient status is a factor, any reconstruction similar to those presented here should be viewed as giving an estimate of metabolic potential, which may differ from actual metabolism to the extent that enrichment can raise the metabolic baseline or alter rates of recovery following disturbance. Monitoring data support the assumption that the South Platte River at our study location has been nutrient-saturated over the last 40 years; corresponding nutrient data are not available for the entire 70-year record of flow, but the fact that the Denver Metropolitan area lies entirely within the catchment of the South Platte River makes it unlikely that nutrients have been limiting to photosynthesis at any time during the past 70 years. Even if nutrient limitation were likely at some time during this period, the main goal of our reconstruction is to evaluate the likely effects of flow management on ecosystem metabolism

in the South Platte River rather than to provide a substitute for long-term monitoring of metabolic rates.

Photosynthesis and respiration were reconstructed on a daily basis from the elapsed time since the last episode of widespread bed movement, which was calculated from the 70-year flow record and the relationships between time since disturbance and rates of metabolism (Fig. 7). The result is a reconstruction of photosynthesis and respiration for the 70-year record (Fig. 8). For the growing season (May–October), reconstructed rates of P and the daily P/R ratio are much lower for recent years (after 1970) than for years prior to 1960; the pattern is similar for rates of R , although the decrease in R since 1960 is smaller than the decrease in P or in the P/R ratio.

Discussion

Shields stress and ecosystem metabolism

Hydrological variability can have a strong effect on rates of ecosystem metabolism in running waters, especially if changes in discharge are of sufficient magnitude to induce movement of the bed (e.g. Biggs & Close, 1989; Young & Huryn, 1996; Uehlinger, 2000, 2006). In the South Platte River, temporal variation in rates of ecosystem metabolism (Fig. 6) is controlled by the relationship between discharge and bed movement, the effects of bed movement on rates of metabolism, and the patterns of metabolic recovery following movement of the bed. Above a threshold of approximately $11 \text{ m}^3 \text{ s}^{-1}$, only a small fraction of the wetted channel is stable and the rate of photosynthesis for the river is near zero. Following a flood that mobilizes a large fraction of the bed, full recovery of photosynthesis may require >10 days (Fig. 7). Thus, at flows below $11 \text{ m}^3 \text{ s}^{-1}$, the areal rate of photosynthesis varies in response to the proportion of the bed that is in motion and in relation to the state of recovery of the periphyton community. Because the recovery of algal biomass does not occur instantaneously, the rate of photosynthesis immediately (i.e. within 1–2 days) after a large flood will be near zero, even if a substantial fraction of the bed is stable at that time.

Photosynthesis and respiration differ in response to bed movement (Fig. 6) because photosynthesis, a sediment–surface phenomenon, is dependent on physical stability of particles that are exposed to sunlight, whereas respiration can occur deep within

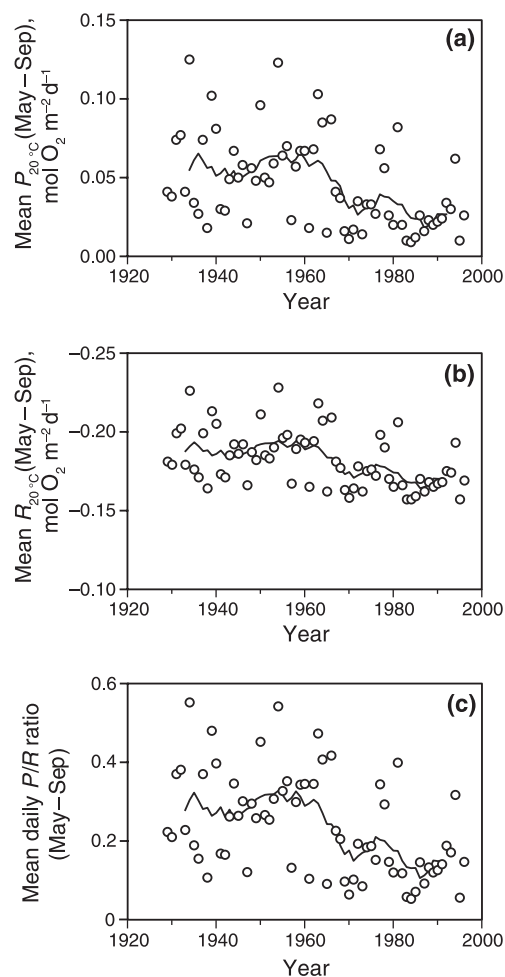


Fig. 8 Reconstructed photosynthetic potential (a) and respiration (b) over the 70-year period of daily recorded discharges in the South Platte River near the study site (growing season: May–September). (c) Reconstructed ratio of photosynthesis to respiration (P/R) over the 70-year period of discharge record. The solid lines show 10-year moving averages.

the sediment profile, much of which is undisturbed by typical bed movement (0–30 cm; Fig. 4). Uehlinger (2000, 2006) also has shown that rates of photosynthesis usually are affected more strongly by bed movement than rates of ecosystem respiration. To the extent that rates of respiration within the sediment column are dependent on organic matter produced *in situ* (photosynthesis), effects of bed movement on rates of photosynthesis may indirectly affect rates of respiration. Because of the differential responses of photosynthesis and respiration, episodes of bed movement strongly suppress the autotrophic function (synthesis of organic matter through photosynthesis),

thus moving the system to a more heterotrophic status (dominance of respiration over photosynthesis) until recovery of photosynthesis can occur through re-growth of photosynthetic biofilms.

Given suitable flow conditions for development of algal biofilms, rates of recovery for photosynthesis will vary in response to availability of nutrients, light and temperature (e.g. Young & Huryn, 1996; Uehlinger, 2000). In the South Platte River below Denver, nutrient concentrations are high, the channel is only slightly shaded (Fig. 1), and, for half of the year, temperatures remain warm. From May through September, rates of photosynthesis and respiration approach pre-spate values within approximately 2 weeks if flows remain below the threshold for widespread bed movement (Fig. 7). Uehlinger (2000, 2006) reported rates of recovery of 2–3 weeks for the Thur River in Switzerland, where nutrient concentrations are lower than in the South Platte River. In the River Necker, Switzerland (Uehlinger, 2000) and in St Vrain Creek, Colorado (McCutchan, 1999; J. McCutchan, unpublished data), recovery of photosynthetic rates following episodes of bed movement took longer still (up to several months) and rates of metabolism were much lower than in the South Platte River. Nutrient concentrations in the River Necker and in St Vrain Creek were much lower than in the South Platte River and, especially for some reaches of St Vrain Creek, mean annual temperature was lower and the channel was more heavily shaded than in the South Platte. Surprisingly, photosynthetic rate was not correlated with the length of time since bed disturbance in the Rio Mameyes (Ortiz-Zayas *et al.*, 2005), although grazing pressure may have been high enough in this tropical river that the sequence of recovery was not easily observed. Thus, interannual variation in rates of ecosystem metabolism for streams and rivers depends not only on the frequency and intensity of bed disturbance, but also on the maximum (potential) rates of metabolism and on the rates of recovery following bed disturbance (e.g. Uehlinger & Naegeli, 1998).

During the initial phase of recovery following spates $>11 \text{ m}^3 \text{ s}^{-1}$, rates of respiration were more variable than rates of photosynthesis (Fig. 6); within the first week of recovery following bed-moving spates, temperature-adjusted rates of photosynthesis were quite low (typically $<0.1 \text{ mol O}_2 \text{ m}^{-2} \text{ day}^{-1}$) but rates of respiration included the highest and lowest

temperature-adjusted rates recorded during the study (Fig. 7). High estimates of the respiration rate shortly after periods of high discharge probably are related to rapid changes in the rate of groundwater flux that occur when discharge is unstable (i.e. when discharge is rising or falling rapidly). When discharge rises rapidly in this reach of the South Platte River, there typically is a net flow of water from the channel to the alluvium ($Q_g/A < 0$); when discharge falls rapidly, as it often does just after a spate, much of the water stored temporarily in the alluvium during rising discharge (bank storage) returns to the river ($Q_g/A > 0$; Pribyl *et al.*, 2005). Then, as discharge continues to fall, the rate of groundwater flux gradually declines to values typical of baseflow conditions (Pribyl *et al.*, 2005). It is possible that high rates of groundwater flux associated with rapidly falling discharge augment the supply of labile carbon to heterotrophic biofilms, thereby increasing the rate of respiration just after a spate (see Roberts, Mulholland & Hill, 2007). Alternatively, changes in the direction and rate of groundwater flux could affect the redox state within the sediments and also the balance between aerobic and anaerobic respiration. If the change in direction of groundwater flux associated with increasing flow temporarily recharges deeper layers of the sediment with oxygen from the channel, flux of water from the channel into the sediment may temporarily increase the areal rate of aerobic respiration within the sediment column. It is also possible that high variability in estimates of respiration during the first week of recovery following bed movement is methodologically driven. Open-channel estimates of respiration are more sensitive to uncertainty in groundwater flux than are open-channel estimates of photosynthesis (McCutchan *et al.*, 2002). During extended periods of low and constant discharge, the rate of groundwater flux in this reach of the South Platte remains quite stable, but Q_g/A can change rapidly during and just after a spate, and uncertainty in Q_g/A can be high when discharge is rising or falling rapidly (Pribyl *et al.*, 2005); thus, estimation of respiration may be affected by uncertainty in the rate of groundwater flux during the early stages of recovery following a spate.

Rates of metabolism are presented here in areal units (i.e. $\text{mol O}_2 \text{ m}^{-2} \text{ day}^{-1}$), rather than longitudinal units (i.e. $\text{mol O}_2 \text{ km}^{-1} \text{ day}^{-1}$). Rates normalized to area are more easily related to concentration (e.g. for a

study of the effects of change in metabolic rate on the concentrations of dissolved oxygen), but rates normalized to channel length may be more appropriate for some applications (e.g. for a study of the supply of organic matter to large, mobile consumers). Choice of units does not, however, affect the overall conclusions of this study. Although channel width increases with discharge in our study reach, the two approaches (areal versus longitudinal units) produced similar relationships between rates of metabolism and the time since disturbance and also produced similar patterns for the reconstructions. The proportional decline in rates of metabolism was similar regardless of the units that were used in calculations.

Concentrations of benthic chlorophyll *a* were measured on only one date, but these measurements (Fig. 5) support the assumption, based on Eqns 1 and 2, that the critical flow depth (h_c ; the depth above which there should be very little bed transport) is 0.20 m. Where the depth exceeded about 0.2 m, chlorophyll concentrations were consistently low; at depths <0.2 m, concentrations of chlorophyll were variable. The abrupt threshold that is apparent in Fig. 5 (i.e. the highest observed chlorophyll concentration occurs at a depth just below 0.2 m) suggests that sediment transport places an important limit on algal biomass in this reach of the South Platte River, but some low concentrations of chlorophyll at depths <0.2 m demonstrate that bed stability at the time of sampling is not the only determinant of algal biomass.

Calculations derived from the expected threshold for widespread bed movement predict that the photosynthetic rate will approach zero at a flow of approximately $11 \text{ m}^3 \text{ s}^{-1}$. Empirical data presented in Fig. 6 suggest that this threshold could be as low as $10 \text{ m}^3 \text{ s}^{-1}$. Although these values are not identical, they are quite similar and the effect of such small variations in the expected threshold for widespread bed movement would have little effect on the overall pattern for reconstructions of metabolism (Fig. 8). If the threshold for bed movement (i.e. the point above which the photosynthetic rate is zero) is set to $10 \text{ m}^3 \text{ s}^{-1}$, rather than a threshold of $11 \text{ m}^3 \text{ s}^{-1}$, the predicted annual rate of *P* is reduced for any given year in the reconstruction, but the patterns for reconstruction are essentially unchanged.

Variation in implicit reach-length with changing discharge has the potential to affect open-channel estimates of stream metabolism when measurements

are made at a single station. For this study, channel dimensions (i.e. average depth for a particular discharge) remained similar for approximately 900 m above the sampling location, and channel slope and reaeration coefficient remained similar for approximately 2 km. Over the relevant range of flows for this study (i.e. $1\text{--}11 \text{ m}^3 \text{ s}^{-1}$), the implicit reach-length varied from 141 to 373 m; thus, the effects of changes in implicit reach-length on estimates of metabolism probably were small. Furthermore, changes in implicit reach-length did not account for the decline in photosynthetic rate with increasing discharge. The slight increase in depth (<15%) just upstream of the reach where detailed measurements of bed topography were made would increase rather than decrease estimates of metabolism as discharge approached $11 \text{ m}^3 \text{ s}^{-1}$. Although the implicit reach length can exceed 1 km at flows well above $11 \text{ m}^3 \text{ s}^{-1}$, the photosynthetic potential under such flow conditions is very low, and any errors in estimation of metabolic rates at flows above $11 \text{ m}^3 \text{ s}^{-1}$ would not have affected reconstructed rates of photosynthesis (Fig. 8).

Ecological effects of water management

Water management is well known for truncation of high flows (e.g. Poff *et al.*, 1997), suggesting that photosynthesis, which is suppressed by disturbance,

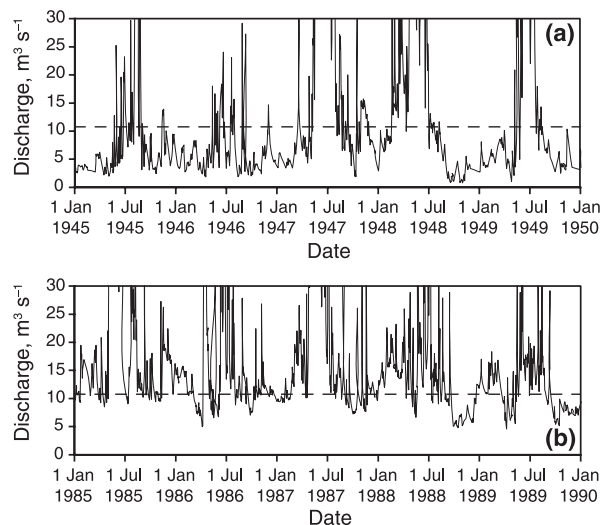


Fig. 9 Discharge of the South Platte River near the study reach for a representative 5-year interval prior to 1960 (a) and after 1960 (b). The dashed line shows the threshold for widespread movement of the bed. Data are from the U.S. Geological Survey (USGS 06721000).

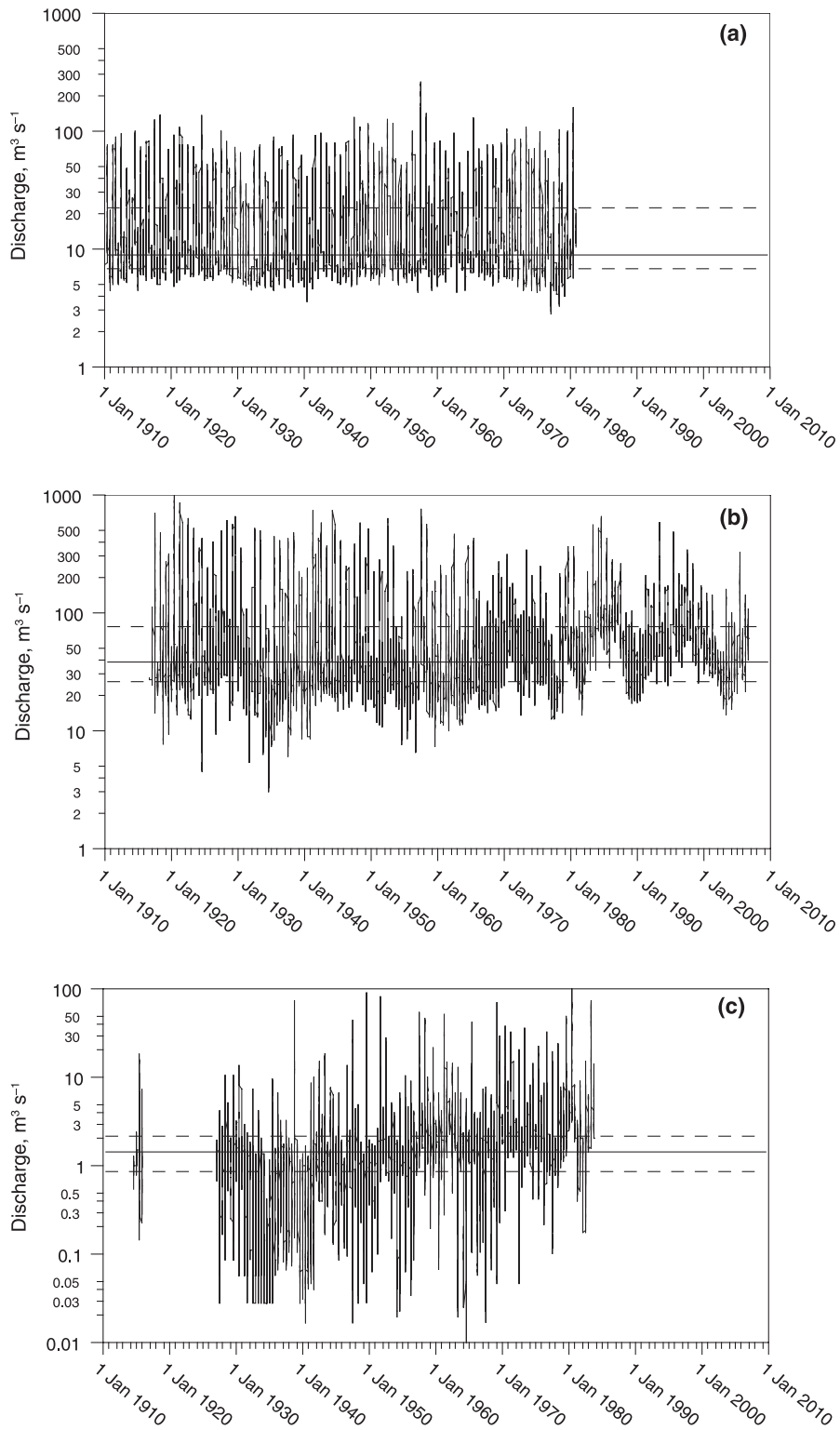


Fig. 10 Long flow records for three gaging stations in Colorado: Arkansas River at Salida (a; U.S. Geological Survey 07091500), Gunnison River near Grand Junction (b; U.S. Geological Survey 09152500), and Big Thompson River near mouth (c; U.S. Geological Survey 06744000).

would be enhanced by water-management practices. Dams can have profound effects on the productivity of tailwater reaches. Operation of the Glen Canyon Dam on the Colorado River (Arizona, U.S.A.) has reduced the frequency and magnitude of bed movement below the dam, and also has resulted in increased water clarity, higher winter temperatures, and increased nutrient concentrations; as a result of these changes, biomass (ash-free dry mass) of attached algae just below Glen Canyon Dam now commonly exceeds 10 g m^{-2} (Blinn *et al.*, 1998; Benenati *et al.*, 2000). Although physical and chemical changes related to dams can dramatically affect the biomass and production of algae and bryophytes immediately below dams, effects of dams on benthic primary producers can be moderated downstream due to inflows of unregulated tributaries (e.g. Munn & Brusven, 2004). Rather than an increase in rates of photosynthesis, the 70-year reconstruction for the South Platte shows that photosynthesis under present conditions is approximately one-third of the amount prior to 1960. This counterintuitive result is explained by a human-induced change in the shear-stress regime.

In the South Platte River, water management has reduced the highest flows, but also has augmented the lowest flows (through wastewater disposal and augmentation of dry season water delivery to downstream sources; Saunders & Lewis, 2003). The overall effect of water management has been maintenance of mean dry-weather flows that are well above those in the river prior to 1960 (Fig. 9). Thus, the increment of discharge that is necessary to raise most of the riverbed to the critical shear stress is much smaller now than it was prior to 1960. Consequently, the frequency of bed disturbance has increased greatly (see Townsend, 1989); virtually every thunderstorm produces a significant bed disturbance. The South Platte River today remains in early stages of recovery from the most recent disturbance throughout most of the growing season, whereas the South Platte River in its more natural state passed through intervals of many weeks over which there was no disruption of photosynthesis through bed disturbance. Because respiration is much less affected by bed movement, the strong suppression of photosynthesis by bed movement has converted the South Platte River at the study site to a much more heterotrophic (net consumer) status (Fig. 8).

Changes in flow management have affected the hydrological regime of rivers across Colorado and in many parts of the world. In addition to the South Platte, long flow records exist for several rivers in Colorado (e.g. Fig. 10) and some of these show clear evidence of altered hydrological regimes. Despite the effects of the Fryingpan-Arkansas Project, which includes Sugar Loaf Dam and the Mt Elbert Conduit, the Arkansas River near Salida, Colorado has not shown substantial changes to the hydrological regime over a 70-year period of record. In contrast, the Gunnison River near Grand Junction, Colorado has seen a general increase in base flows and some truncation of peak flows since Blue Mesa Dam was completed in 1965. The hydrological regime of the Big Thompson River has been greatly affected by the Colorado-Big Thompson Project, which includes diversion of water from the Colorado River to the Big Thompson. Knowledge of the specific relationships between discharge and bed movement would be required to make predictions of the consequences of hydrological change on metabolic rates in these or other rivers, but human-induced hydrological changes are widespread and metabolic rates in many rivers may have been affected by these changes.

Other applications of the method

This study shows the power of Shields stress as a means of reconstructing some important ecological effects of hydrological change in streams and rivers. Similarly, the Shields stress could prove to be a valuable tool in anticipating the effects of changes in climate or land use on flowing-water ecosystems or in exploring hypothetical flow regimes that may be achieved through water management for restoration purposes (Ward *et al.*, 2001) or as an inadvertent by-product of water-management practices that promote various uses of water.

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